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On the Biology of Fomes Applanatus (Pers.) Wallr.

BY

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A Thesis submitted in conformity with the requirements for the Degree of Doctor of Philosophy in the University of Toronto.

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I. INTRODUCTION.

The most important agents responsible for the decay of wood substance in our forests and elsewhere are undoubtedly those plants comprising the autobasidiomycetous group of fungi, and of these the polypores cause the most destruction. The foundation work in this field was laid by R. Hartig, and he has been followed by many investigators both in Europe and in America—von Schrenk, Spaulding, Meinecke, Hedgecock, Long, Weir, Ward, Münch, Faull, Atkinson, Buller and others. While much of the work of these investigators would probably

be substantiated by more exacting methods than they have employed, there is one general weakness in method throughout in that the identification of causal agents has been carried out almost solely on the basis of propinquity of fruiting bodies; in contrast to the investigations of other plant diseases there has been very little work by the application of bacteriological methods—establishment of cause and effect by cultures and inoculations—at least, there is very little indication of this in the literature published on the subject.

Among the many polypores that attack our structural and standing timber there is none more conspicuous owing to the large size of its perennial applanate brackets, or more frequent, than the species *Elfvingia megaloma*, more generally known as *Fomes applanatus*. It is very widely distributed, being found throughout Canada and the United States, and within this territory is of very common occurrence. In the hardwood localities where it occurs its fruiting bodies are to be seen in great abundance on tree trunks, stumps, dead stubs and logs. It grows more frequently on deciduous than on coniferous species, and while it usually attacks dead wood it is also found quite extensively on living trees. With its wide distribution, common occurrence and rapid growth, it is responsible for the decay of very large quantities of wood annually. Because of its frequency, many references are made to this fungus, but, strangely enough, aside from Heald's studies (20) on its relation to a disease of cottonwood, no intensive investigation has been heretofore undertaken on this form. This may be accounted for by the fact that its ravages in Europe do not appear as great as in America, consequently receiving little attention there, or because of the reiteration of statements of opinion expressed by certain pathologists that the fungus is a pure saprophyte. To this must be added the very important fact that in dealing with the question of parasitism versus saprophytism of wood destroying forms there have been so far no reliable criteria for distinguishing between the two, and so there have been meagre grounds for combating any widely accepted view either one way or the other.

The present investigation on *Fomes applanatus* comprises three main lines of inquiry—a study of the action of the fungus, a determination by the application of cultural methods as to whether it is really responsible for the rot features it seems to cause, and to investigate in relation to the larger subject of host relationship the possibility of finding some reliable and definite criteria by which we may distinguish parasitic action on wood from saprophytic.

II. SPECIES INVESTIGATED.

(*a*) *Identity:* Like many other plants of wide geographical range this fungus exhibits considerable variation in its morphological characters, and at times its identity with the north European *Fomes applanatus* has been questioned. Thus Murrill (30) considers it an entirely distinct species—a position based on the creation of the species *megaloma* in 1846 by Léveillé (23) on material sent him from north-eastern America. It is of interest to note in this connection that Léveillé found specimens in the same consignment which he regarded as being identical with the European *F. applanatus;* that is, in one lot of American plants sent to him he regarded some as being identical with the European *F. applanatus* and others as belonging to a new species, restricted to America, and named by him *Polyporus megaloma*. The differences noted by Léveillé had to do with the colour of the cap and the pores and the width of the sterile border underneath. However, American mycologists (including Murrill) today consider that Léveillé was wrong in so far as he recognized two species from America, and hold that all of our plants belong to the same species whatever we may call it. A study by Atkinson (2) in 1908 would appear to establish its identity with the European form, thus reducing *P. megaloma* to a synonym—a view contrary to that held by Murrill, as already stated, who regards our form as different from the European and restricted to America. The writer has examined hundreds of fruiting bodies in this region, and finds that the characters of the fruiting body are fully as variable as stated by Atkinson. In particular there is much variation in the width of the sterile band, as illustrated in Fig. 1; moreover on the same pileus the band is wider early in the growing season than later; it is generally wider in one year old pilei than in older ones; occasionally one finds narrow- and wide-banded punks growing mixed on the same log, though this is not the rule. Further, an examination of the Sydow European material in the herbarium of the University of Toronto has brought out no criterion for separating it from the New World form. Neuman (33) in a very recent study, also considers our species identical with the European. A careful weighing of the evidence seems to show that there is little doubt of the identity of the European and the American forms, at least as yet no constant feature has been described that would distinguish between the two, and I quite agree with Atkinson in relegating *P. megaloma* to the rank of synonymy and in calling our plants *Fomes applanatus*.

(*b*) *Hosts:* Various partial lists of hosts are on record by different writers. Farlow and Seymour (14) in their Host Index recorded *Acer*

nigrum, *A. saccharum*, *Quercus alba*, and *Tsuga canadensis*. Hedgecock (21) gives the most complete list, including species of *Acer*, *Alnus*, *Betula*, *Crataegus*, *Fagus*, *Fraxinus*, *Hicoria*, *Liriodendron*, *Morus*, *Nyssa*, *Populus*, *Pyrus*, *Quercus*, *Salix*, *Robinia*, *Tilia*, and *Umbellularia;* and of conifers, *Abies*, *Picea*, *Pseudotsuga* and *Tsuga*, or 53 species in all. Atkinson (1) Spaulding (45), Weir (50), Rhoads (39), and others, also record in one connection or another the occurrence of *F. applanatus* on certain species belonging to some of the genera named above.

In this region, this fungus seems capable of destroying the wood of any species of deciduous tree, and a list of its hosts includes practically all the species of our local flora. To these are to be added three species of conifers, viz.: *Tsuga canadensis* (stumps and wood on the ground, in localities near Toronto); *Pinus Strobus* (planking supporting a lawn, Toronto); *Picea* (probably *P. rubra*—bridge timber in Adirondacks, N.Y., collected by Professor J. H. Faull, and dam timber in Quebec, collected by Mr. A. W. McCallum.)

While there are many references scattered throughout the literature with regard to the association of *Fomes applanatus* with living trees, no lists, with the exception of some incidental records, have been published from this distinctive point of view. Heald (20) in 1906 reported finding it on cottonwood. Neuman (33) records it on apple, oak, cottonwood and willow; while Hedgecock (21) enumerated *Liquidambar styraciflua*, *Pyrus malus*, *Morus rubra*, *Populus tremuloides*, *P. trichocarpa*, *Quercus rubra*, *Acer saccharinum*.

My list of its occurrence on living trees includes the following species:

Acer saccharinum.
A. saccharum.
Aesculus kippocastanum.
Betula alba var. papyrifera.
B. lutea.
Carpinus caroliniana
Fagus atropunicea.
Gleditsia triacanthos.
Liriodendron tulipifera.
Morus alba.
Populus alba.
P. balsamifera.
P. grandidentata.
P. nigra var. italica.
Pyrus aucuparia.
Quercus rubra.
Q. velutina
Robinia pseudacacia.
Salix nigra.
Tilia americana.
Ulmus americana.
Cultivated varieties of *Malus.*
Cultivated varieties of *Prunus.*

(*c*) *Related Species:* The genus *Elfvingia*, as defined by Murrill (30) includes several other representatives in America, and it is interesting to

note that there is good reason for thinking that at times all of these may be parasitic. Two of them, *E. fasciata* and *E. tornata*, are tropical or subtropical forms, appearing to replace respectively the northern *fomentaria* and *applanata*. Of *E. tornata* little is known, though said to be common on deciduous wood and widely spread throughout the tropics; Petch (37) reports that "as a rule it is merely saprophytic (in Ceylon) but several instances have been noted in which it is a wound parasite", notably on *Acacia decurrens*. A form from Nicaragua and Panama standing very close to *tornata*, if indeed distinct, has been differentiated as *E. Lionnetii*. Fawcett (16) has reported that *E. fasciata* is frequently a parasite of orange trees and water oaks in Florida; it also occurs on dead wood. *E. lobata*, a species found from New York to Iowa and south, but so far not recorded for Ontario, occurs on diseased trunks of certain deciduous trees, especially the white oak, as well as perhaps more commonly on dead deciduous wood. Of it Murrill (30) says, "Facts thus far collected indicate that *E. lobata* is a southern form and confined to a much more restricted area than *E. megaloma*, while within this area it is often abundant and quite destructive to the oak, its favorite host." *E. fomentaria* (recently elevated to a new genus, *Elfvingiella*, by Murrill on account of the hyaline character of its spores) very abundant in Canada and the United States, especially on birch and beech and sometimes maple and poplar, is regarded as a parasite by American pathologists. It also is native to temperate Europe, where it has long been regarded as a parasite on the hardwoods. Thus, whatever we may consider *Fomes applanatus* to be, there is a general uniformity of opinion that the species commonly grouped with it are to be classed as wound parasites. A return will be made to this subject later on in this paper, but an account will first be given of cultural studies and of the biology of the spore.

III. SPORE STUDIES

My investigations on the spores have revealed many features of interest, especially in connection with their organization and their discharge. I have found no spores of any kind produced by the mycelium either in nature or in cultures, nor are there any references to such elsewhere in the literature. Some observers have claimed that there are conidia growing on the upper surface of the pileus—referred to here in the section entitled "Secondary Spores"—but so far as my observations go there are none but basidiospores and these are borne only on the walls of the pores where they regularly belong.

(a) *Spores:* The basidiospores are unicellular, 7-9 μ. long by 5-6 μ wide, and dull reddish-brown in colour. They are broadly ovate with one side more convex than the opposite half and the apex broadly conical but in dried spores appearing truncated. A very large central globule is present. The spores are smooth according to some writers and echinulate according to others. Atkinson (2), who was the first to investigate the nature of the spore wall, says: "The spore wall is hyaline or nearly so, with numerous perforations into which it appears that the brown or yellowish brown content of the spore projects." According to him those who have described the spores as echinulate have been misled by the appearance of the numerous dark ends of the perforations as seen in a surface view of the wall, which he holds to be thick as well as hyaline. But a study of the spores shows that Atkinson has not properly interpreted their structure. In studying their development, we find that the basidiospore starts out with a thin hyaline wall, and then that later within this original thin hyaline walled basidiospore a rough coated, thick and yellow walled endospore is formed. The spore "wall" in one sense then is accordingly double. As the endospore is more shortly elliptical than the original basidiospore, the tip of the latter is not occupied and this hyaline tip being thin walled and without supporting contents usually collapses. This gives to the mature spore the "truncated" appearance so invariably noted.

Regarding the attachment of the spores two views have been held. Various mycologists have assumed that the spores were attached by their narrow-pointed ends to the sterigmata, since their descriptions regularly speak of ovoid spores, "truncate at the base." This view has been taken by Patouillard (36), Bresadola (8) Murrill (31), Overholts (34), and others. Atkinson, however, on critically examining the shapes of discharged spores, concludes that the older views are wrong, that the narrower end is the apex or distal end, and that the spore is "attached to the sterigma by the side of the broad end opposite the more convex side of the spore." One wonders whether any of these botanists ever observed the spores *in situ;* for razor sections made through the new spore layer of an actively sporulating fruiting body reveal spores in all stages of development attached to basidia, leaving no question as to the mode of their attachment, and establishing by direct observation the correctness of Atkinson's conclusion that the so-called "truncate base" is in reality the apical end of the spore.

(b) *Sporophore:* The sporophores of *F. applanatus* are perennial and a new tube layer is formed during the growing season of each year of its life. In nearly all cases a tube layer is formed sometime during the

first season, the time of its formation being contingent on the organization of the contextal foundation on which it is laid. The sporophore may vary in width from an inch or two up to four or five inches before the tubes appear, and may attain a growth of eight inches in width and five inches in depth before the end of its first season. The life of the sporophore is short when compared with such a form as *F. igniarius*, in some fruits of which as many as 80 annual layers have been counted (3). The fruiting bodies of *F. applanatus* under apparently normal conditions may die at the end of the second or third year, recalling in this respect its close relative *F. lobatus* which lasts but a single season, but which organizes, however, a new pileus immediately beneath the dead sporophore of the preceding year. The average life of the sporophores of *F. applanatus* in this region is four or five years, though occasionally one may find fruiting bodies showing as many as eight or ten layers of pores.

The organization of the second and succeeding pore layers is almost unique in that the layer is initiated by the formation of a sterile layer which completely covers the exposed surface of the pores of the preceding season; it is on this layer that the new pores are formed. Of our native perennial polypores *Fomitiporia laminata* is possibly the only other one that exhibits such a phenomenon. This layer begins to form with the opening of the growing season, and by the end of April the pores are indicated. In this locality a tube length of 1/16 inch is commonly found by the first or second week in May, and the fall of spores from the new hymenial surfaces has already commenced. In this connection it may be stated that Buller (10) found *P. squamosus* discharging spores when the tubes were only 1 mm. long. The growth rate of the tube layer is at first comparatively rapid, the layer often measuring 3/8 inch in thickness by the end of July; after that growth slows down very considerably, gradually becoming imperceptible. It may be presumed, however, that some growth continues to take place throughout the rest of the season.

c) Spore Production and Discharge: As an essential part of my studies on the spore production and spore discharge of *Fomes applanatus* continuous observations were made on the same fruiting body throughout the years 1915 and 1916, extending over the full twelve months of each year. From early spring until late in autumn spore traps were set daily under this one sporophore; during the winter months the spore traps were exposed without interruption, but were collected weekly instead of daily as it was found that daily visits were entirely superfluous. In addition to the unbroken series of observations on this one fruiting body throughout two consecutive years, collections of data relative to spore discharge were made regularly for longer or shorter periods of time during the summer months from many other specimens.

One of the most noteworthy results of this work has been the c covery that the period of spore discharge begins early in May and c tinues without interruption up to the first heavy frost in late October early November, when it suddenly ceases (except for a few spores wh may fall any time throughout the winter and to which further referen will be made), and in this respect establishes a new record. Spore d charge, in brief, in the case of *Fomes applanatus* continues for appro mately six months—probably a new record for all fungi. The cl approach to this prolonged spore fall for a polypore under natural co ditions known to the writer is the case of *Polyporus squamosus;* in whi species Buller was astonished to find discharge going on for sixteen da and estimated three weeks as the probable limit. During this period approximately six months the liberation of spores apparently nev ceases, and is remarkably uniform. When spore fall first commenc the deposit is rather scanty for a few days, but even then is quite evide to the unaided eye. Soon, however, a degree of daily deposit is reach which does not seem to vary much for the balance of the season. A increase that may be observed is in the months of July and Augu The daily slide collections for two seasons showed invariably their usu coating. Changing slides at regular intervals throughout the day an even throughout the night likewise gave no indication of any periodici of discharge. Day and night throughout the season the process of di persal seems continuous. On a still day one may readily see the spo drifting away from a fruiting body in curling clouds like wreaths of ve fine smoke as long as one cares to watch them. I have observed these the field as late as October 15. Night examinations of spore clouds we made with no other special apparatus than that of a lantern

From these facts it is apparent that the number of spores liberat is beyond comprehension. The phenomenon of spore clouds visible the unaided eye alone indicates their countless numbers. The ma caught on a glass slide in 24 hours is ordinarily sufficient to render opaque. Buller, from a count estimate in the case of *Polyporus squa mosus*, a form which also exhibits spore clouds, concluded that at lea 1,700,000 spores were discharged from one tube in three days. A simil calculation with *F. applanatus* gave the incomprehensible number 30,000 million spores liberated in 24 hours from a fruiting body with pored surface of about one square foot. Now, as there may be hundre of equally active fruiting bodies to the acre in many forest areas, espe ially where there is much fallen timber—the writer has counted as man 60 average sized active fruiting bodies of *F. applanatus* [illegible] ly in the wood [illegible] appreciate the [illegible] with which [illegible]

spores will drift into places where conditions are favorable for their germination and growth; and of the chance that the infection will be able to establish itself in any susceptible tree.

But spore discharge over such a long stretch of time as six months, characterized by neither diurnal nor seasonal periodicity, means more than an enormous crop of spores; it also implies a pronounced tolerance of the sporophore to changes within wide limits in such environmental factors as light, temperature and humidity. That the sporophores of *F. applanatus* develop normally in total darkness we know from Spaulding's observations on mine fungi (46). That spore discharge is immaterially affected by weather conditions in general is borne out by our own observations on identical fruiting bodies during the season of 1915 and 1916, which were markedly different climatically in this region. The year 1916 began with a rather backward spring and continued cold and wet until the end of June, but was followed by an unusually hot and dry summer; while in 1915 there was an average spring followed by a summer of average temperature but high precipitation. Yet from day to day throughout both seasons, even on successive days of contrasting weather, the density of the daily brown deposit on the glass slides set as spore traps essentially remained the same, so far as could be judged without actually counting the spores.

Also, temperature changes, except within very wide ranges, did not appear to affect spore discharge. For instance, collections made half-hourly one night in late August from 9.10 p.m. to 9.30 the next morning, with temperature changes from 9° C. down to 3° and up again to 15° showed a uniform copious deposit. The discharge however is stopped by a freezing temperature; and this appears to be an unusual phenomenon among polypores. I have not been able to find any previous record where spore fall in a polypore is abruptly terminated by frost. In this connection it may be noted that Buller (11) found that some Hymenomycetes continued to shed their spores at the freezing point of water, though at a very diminished rate, while Overholts (33) as well as Buller states that the fruiting bodies of many Polyporaceae gathered in midwinter (January and February) throw an abundance of spores when brought into the laboratory. It is true that throughout the depths of winter a very few spores were invariably found on my slides left for a week under a fruiting body of *F. applanatus*, but there was good reason to believe that these were spores that had lodged and had mechanically fallen out after their exterior surfaces had lost their natural adhesiveness. This loss of adhesive power is exhibited in the case of spore deposits on slides kept in the laboratory, and lodged spores are to be seen at any time

in the winter in razor sections of the tubes. At any rate the fact rem
that spore discharge is copious up to the first hard frost, and that
sequently it is inconsequential no matter how mild the weather ma

Variations in atmospheric humidity likewise were not reflecte
fluctuations in spore discharge, an observation in harmony with
of Buller (11) on *P. squamosus* who could detect no change in spor
when the surrounding humidity was greatly changed. Spore disch
however, is greatly affected by one factor other than frost, and
is the moisture content of the sporophore. When this is lowered b
a certain minimum spore production is checked, and is not resume
the normal rate until the necessary amount of water is restored. Fru
bodies in unshaded positions in dry weather throw spores sparsely
no doubt the explanation of this is to be looked for in their low mois
content. It further happens occasionally that sporophores growing u
favorable conditions produce few spores or none at all. It is not
probable that such sporophores are naturally sterile—a phenomenon
has been observed in *Coprinus*, *Agaricus*, and other genera

d) Secondary Spores: Although secondary spores are prod
by comparatively few Hymenomycetes, *Fomes applanatus* is state
produce conidia on the dorsal surface of the pileus. Schulzer
Muggenberg (42) was the first to make this statement in 1880.
Murrill in his specific description says that the upper surface of
fruiting body is conidia-bearing and usually brownish during the gro
season from the covering of conidia. This brown coating is in
frequently to be seen, but examination showed that in every case it
composed of basidiospores. These are mechanically deposited by
currents of air after they fall from the hymenial tubes. This ca
easily proved in such a case by covering the top with a sheet of pa
which soon bears the same coating of spores. Moreover, the upper
is of such an organization as not to favour spore production, beco
heavily encrusted during its first season. Young fruiting bodies i
stages of development, as well as very many others of various ages,
been persistently examined in the field for conidia, but without suc
Likewise none of my artificial cultures produced conidia

e) Spore Germination: In the germination studies the usual han
drop method with Van Tieghem cells was used. Various media
tried, including distilled and tap water, solutions of grape sugar,
sugar, maltose, peptone, meat extract, acids, alcohol, alkalies, etc
graded percentage strengths. Decoctions of wood and hanging d
of water containing pieces of wood were also experimented with.
greatest success was attained with two brands of domestic malt ext

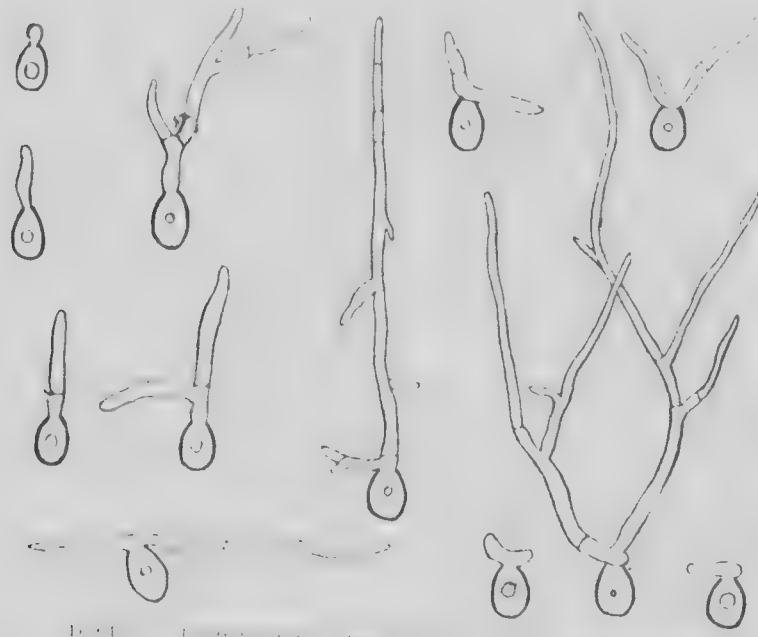
put up for invalids, but then only with the spores from some of my traps. The percentage of germination at best, however, was always low, usually a fraction of one per cent. No difference was observable in the appearance of those spores which would germinate and those which would not; nor between those taken from traps with viable spores and those from traps with none but non-viable spores. Spore collections which exhibited viability in the above mentioned malt extracts would also germinate at times in distilled or tap water, on potato agar, and on moist sterilized wood. This behaviour differs from that of spores of *P. squamosus*; Buller (10) was able to germinate these in a malt-wort extract but not in water or on fresh wound surfaces.

The most puzzling behaviour on the part of the spores was encountered. The great majority of the collections made on glass slides failed to exhibit any germination. Once one had located a spore slide collection which showed germinating powers one could go on daily for weeks with practically uniform success. Sooner or later, however, germination ceased abruptly. There was no uniformity of age at which viability ended. The oldest viable spores encountered had been kept six and one-half months after collection in a laboratory hotter and drier than most rooms. It may be noted that Price (38) found the spores of *P. squamosus* had lost their viability in 79 days, and Miss Bayliss (4) those of *Polystictus versicolor* between 11 and 17 weeks.

Every conceivable possible factor in the germination was tested out. Most of the experiments were carried out at ordinary room temperature; tests showed no acceleration or retardation by altering temperature conditions between 10° and 27° C. Tests were carried out in bright light, dull light and darkness; spores were given different lengths of time after spore fall to "ripen", before being tested; they were even allowed to undergo freezing outside; they were collected from natural lodgments in the woods at various times and tested immediately. Nor could viable spores be traced to those liberated at any particular period of the sporulating season. The Van Tieghem cells were set up without using vaseline to seal them; the glassware was treated in various ways, being washed in alcohol, or acid, or distilled water; the results were the same. The hundreds of tests with reference to possible controlling factors involved many weeks of labour, and in the end nothing was uncovered that would induce a higher percentage of germination, or any germination at all from many slides. The seemingly erratic behaviour would appear to be explainable only on the grounds of inherent low viability of the spores.

The first signs of germination in the malt extract medium are generally visible in about 24 hours, seldom sooner, when a few spores put

forth their germ tubes (Text Fig. 1). A definite polarity is exhibite
tube always issuing from the "truncated" apical end of the spore
the wall appears to be lighter in color and apparently thinner, and
it almost equals in diameter. In the earlier stages, in general the
two habits observable. In the one the hypha grows out in the dire
of the long axis of the spore for some distance; branching soon comme
though it may be delayed till the leading hypha is some 15 time
length of the spore. In the other type, the hypha at once assu
direction at right angles to the long axis of the spore; branching b
earlier and results on the average in a more symmetrical system.
erally these types are not much mixed in the same culture, as a



appearing in separate cultures. Practically all the germination
obtains in a given mount is in evidence in 48 hours, though a
belated ones are encountered; and since growth proceeds at a fa
uniform rate any particular hanging drop presents a rather defi
picture at any given stage. The spore features and the germina
hyphal system are so characteristic that one readily notices any for
spore or its product

Growth is very rapid, Text Fig. 1 showing an average plant which has attained the size represented 72 hours after the spores were sown in the malt extract. Though cross walls are difficult to discern in the young plant in untreated cell cultures, branching can usually be made out to take place just below a septum. The only change observable in the spore during germination is an immediate reduction in size of the central globule and this reduction in size continues until it finally disappears. The protoplasm of the hyphae is colorless and shows minute highly refractive bodies. After four or five days vacuolation is noticeable in the older cells.

In connection with the germination tests one more fact is worthy of note. In some of the old mounts it was observed that dense fuzzy or witches' broom-like masses appeared on some of the hyphae. The same growths were encountered in some tube cultures. They proved on examination to be made up of very numerous short branches, strictly localized and of such an appearance as to lead one to expect conidia, but none were found. Their significance is unknown. Brefeld (7) noted and figured the same thing.

IV. CULTURAL STUDIES.

a) Historical: Prior to the appearance of Hartig's "Wichtige Krankheiten der Waldbaüme" in 1874 and his "Zersetzungserscheinungen des Holzes" in 1878 but little was understood about the decay of wood; the latter thesis included accounts of seven species commonly attacking coniferous timber and six causing decay in oak. Hartig was the first to associate a specific decay appearance with a particular fungus and in emphasizing this fact he made his most important contribution. His *modus operandi* involved a complete description of the fungus concerned, a minute account of the destruction of the wood, with many illustrations of the progressive microscopic amd macroscopi changes. In no case was there any attempt to establish identity of the causal form by culture or inoculation.

The next contributor of importance in this field was Mayr (26) who in 1884 described in detail the action of two species of *Polyporus* parasitic on birch. But his methods were similar to those of Hartig and likewise included no cultural studies. This statement also applies to most subsequent work; thus in the last fifteen years, while American mycologists have given a very great deal of attention to polypores responsible for the decay of timber and of forest trees, in general the studies have had largely to do with the macroscopic and microscopic changes expressed in

the specific rot or disease, and with preventive measures; little cul work on the causal forms has been done.

In 1897 Ward (49) opened up a new field in connection with the s of wood destroying fungi, by proving that such forms are capab culture. His studies were on *Stereum hirsutum*. He first of all minated the spores on gelatine and agar media, using sugar or r juice as a nutrient, and succeeded in obtaining an abundant grow mycelium: the mycelium obtained in this way was then transferr sterilized blocks of wood kept moist in containers. In the course of four months fruiting bodies made their appearance in his cult abnormal in shape, it is true, but which nevertheless sporulated the first time a basidiomycetous wood destroying fungus was cult on its host from spore to spore. Ward's purpose, however, was m to test the possibility of such artificial cultures. He had not in view demonstration that the features of decay usually associated with fungus were really traceable to it, but rather to show that the cul technique employed in the study of other fungus diseases was like applicable in the study of the diseases of wood.

Contrary to hopes that might be aroused by Ward's success *Stereum hirsutum*, experience has shown that similar attempts higher fungi commonly lead to disappointment, so that, as yet, rep successful cultures, with the sporulating fruiting body as an end atta constitute a very brief list. Little trouble is ordinarily encounter securing spore germination and a growth of mycelium, and it is expected that more intensive effort will reveal the knowledge o environmental factors conducive to fructification. Where time and s are factors, the perplexities of technique are greatly increased, be of the difficulty of preventing drying out or of the introducing int culture new supplies of water and nutrients without permitting a same time the entrance of contaminating moulds or bacteria. I brief review of such work that follows, only the wood-destroying form noted.

Biffen (5) followed Ward's studies in the following year with a count of similar work in relation to the action of *Collybia velutipes* o wood of *Aesculus*. He germinated the spores in hanging drops of sugar solution; the mycelium obtained in this way broke up into chains within nine or ten days, and these were transferred to ster wood blocks. Normal sporulating sporophores were produced wit month. Four years previously Costantin and Matruchot (12) exhibited normal fructifications of this same species obtained on cultures in two months.

Biffen (6) has similarly investigated *Bulgaria polymorpha*. The spores in this case were germinated in beerwort gelatine, and from plate cultures sterile blocks of oak were inoculated; fruiting cups bearing ascospores appeared in three months. His paper gives the action on oak in detail, and the development of the fungus.

Falck (13) in 902, reported culturing three agarics to the fruiting body stage, following in general, Biffen's method.

Among American mycologists excellent work on cultural investigations of xylophilous fungi has been done by Lyman, Spaulding, Buller and Zeller. Lyman's work (25) is by far the most extensive, but as his interest centred in the secondary spores of Autobasidiomycetes, the securing of fruiting bodies was rather incidental. He cultivated some 75 species of Thelephoraceae, Hydnaceae and Polyporaceae from their spores. Unfortunately the bulk of his notes was accidentally lost, but he reports that "in the majority of species studied I was able with more or less difficulty to raise basidiosporic hymenia in the laboratory." Spaulding (43) in 1905 reported culturing *Schizophyllum commune* successfully, but in later cultures of another agaric, *Lenzites sepiaria*, on sterilized pieces of wood he got only abnormal sporophores which he does not mention as sporulating (44). The highly destructive *Lentinus lepideus* was also studied in a similar manner by Buller (9) in connection with a decay of street paving blocks, and with like results. Zeller (51) cultured *Lenzites sepiaria* from spore to spore. Buller (10) has given us a very interesting biological paper on *Polyporus squamosus* including a very detailed account of the structural and chemical changes brought about in maple wood by this fungus, and likewise of the responsible enzymes. Cultural studies were also made, the spores being germinated in hanging drops of malt extract and cultured on extract solidified with gelatine. In nine months, however, there were no signs of any attempt towards the formation of a fruiting body. Later, this species was cultured on blocks of wood by Price (38) who succeeded within six to ten months in getting abnormally shaped fructifications. This, though, occurred only in the case of those cultures kept in dull light, and none appeared in darkness nor in bright light. All his fructifications remained quite sterile. Miss Bayliss (4) has published a biological study of *Polystictus versicolor*, including its destructive action on wood in detail. The cultures on wood blocks produced only abnormally shaped fruiting bodies, sterile even after 17 months. Some of these were induced to sporulate later by removal from their containers and placing outside under natural conditions. So far as I can find *Polystictus versicolor* is the

first polypore to be successfully cultured to sporulation, thou
conditions were not wholly artificial.*

My work on *Fomes applanatus* demonstrates that it now is
added to the list of wholly culturable forms, the first of the *Fom*
carrying through the cultures the procedure was first of all to gr
mycelium on agar in tubes, and then to transfer portions of the my
to sterilized wood in large containers. It was found that the
never fruits on an agar medium. The mycelium was obtaine
three sources: (1) spores, (2) pieces of sporophore, (3) pieces of di
wood, and thus three parallel series of cultures were carried throug

b) *Tube Cultures:* The spores used for starting cultures w
tained from the deposits on slides set in spore traps as already des
These slides were stored in ordinary microscope slide boxes and u
occasion demanded. The glassware used in the germination cel
sterilized, the malt extract was sometimes sterilized and sometimes
it seemed to give a rather higher percentage germination wh
sterilized, and for all practical purposes served equally well, for th
portion of infected mounts in the many hundreds of cells employe
negligible. The hanging drops of the cells were inoculated with ve
spores so that every spore in the mount could be examined as
identity. After germination, with care one plant could be picked o
platinum loop for transference to the agar medium

Many agar media such as oatmeal, wood, acorn, etc., were tri
the best results were obtained with ordinary potato agar. Th
made by soaking 30 grams of shredded agar overnight in one litre of
and replacing the unabsorbed water by strained thick potato wate

Growth is rapid, the threads radiating out regularly, so that
or six days a circular snow-white patch one-half inch in diam
present. In less than two weeks the whole slant face of agar in a
quarter inch tube will be covered. Further growth results in a thic
up of the layer so that the earlier fluffy appearance is somewh
This layer soon becomes woven into a thin leathery sheet which is
enough for the mycelium to be extracted bodily. As time goes
surface takes on a powdery look as if conidia were being form
all my tubes examined none were ever discovered, the powdery
ance being due to the numerous excreted crystals of calcium oxal. t
the witches' broom-like branches

[illegible] Harsch (21) [illegible]
[illegible] on malt and
[illegible]

After about a month's culture the mycelium begins to take on a yellowish tint. Generally this is observable first in the central region, gradually extending to both ends of the sheet. The yellow color darkens, finally reaching a dark brown shade, often with a purplish cast. Usually these progressive color differences are expressed as a zonation. At this time the growth often exudes conspicuous glistening drops of fluid. The mycelium preserves its vitality for many months. Even after the whole culture has shrivelled up hard and dry, new cultures may be started from bits of the sheet.

Tests carefully carried through to the formation of the fruit bodies have shown that the rather tedious spore method of starting cultures could be successfully substituted by the tissue method first described by Duggar, or by using pieces of decayed wood. The easier method was to take pieces from the interior of the sporophore; these could be depended upon to grow readily, and experience brought out the fact that the pieces did not even need to be sterilized by passing through a Bunsen flame, as recommended by Spaulding. In the other method of using pieces of the diseased wood, contrary to expectation, one was seldom bothered with bacteria if the sounder pieces were chosen. Both these methods were very convenient. The characters of the tube cultures derived in either of these two ways differed [illegible] agars tried out it was found necessary to complete the cultures on wood. For this purpose, blocks of wood after being water soaked were placed in jars and the whole sterilized. They were then inoculated [illegible] mycelium from tube cultures, or directly with pieces from the interior of a fruiting body. This latter method is perfectly satisfactory and a time saver. Representatives of practically all the hardwood [illegible] north eastern North America were used, and no difficulty was [illegible] getting the fungus to grow on any of them. Certain woods such [illegible] wood and poplar were found more suitable in that they lent themselves better to the technique, and accordingly these were mainly used in the cultures on wood. Green timber [illegible] acrence. Coniferous wood [illegible]

[illegible] practically immune from destruction by this [illegible];

The carrying of culture on wood through to the production of [illegible] in the case of such a term as [illegible] protected experiment with the corresponding cultures of [illegible] infection from outside and of keeping the wood specimen from [illegible]. At first much time was lost in carrying along cultures which [illegible] dried out in the course of five or six months. Fortunately, the well grown aspen wet wood [illegible] to be in the culture w[illegible] moisture contents, a high percentage of water. In the more [illegible] cases the wet wood mentioned [illegible] were not well [illegible] in the beginning. The wood blocks were [illegible] right color in the volume were put through a water bath [illegible] after each bath and plunged into cold water to drive out all [illegible]. The blocks were placed in the [illegible] containing [illegible] of water and [illegible] phosphate poured over the whole [illegible] months [illegible] by autoclaving for 20 minutes after 12 pounds [illegible] had been reached. During [illegible] the water was usually lost, [illegible] quantity of [illegible] was [illegible] through experience [illegible] importance of the [illegible] the culture [illegible] the culture [illegible] without [illegible] after [illegible]. The [illegible] the [illegible] sterilization, w[illegible] complete [illegible] except for the lower ends and such were [illegible]. Here were [illegible] the [illegible] wet wood particularly. The [illegible] wood [illegible] through [illegible] condition were [illegible] the [illegible] wood, poplar and willow, and [illegible] were [illegible] [illegible] little [illegible] work.

The [illegible] were then [illegible] in [illegible] a couple of weeks [illegible] appeared. The [illegible] wood were then [illegible] [illegible] [illegible] [illegible] culture [illegible] [illegible] wood [illegible] [illegible] [illegible] [illegible]

The growth behaviour on the surface of wood is similar to that on agar. The hyphae grew out from the inoculation material forming white circular patches, steadily enlarging. The fastest rate recorded was one in which a piece of mycelium about 3/8 square inches in size in the course of ten days covered an area of five square inches. Eventually the same color changes ensue as has been noted for the cultures on agar. In the majority of the wood cultures, however, only a small portion of the surface of the block is overgrown by the mycelium. Usually the transferred mycelial bits were placed on the transverse face of the block, and it was found that the hyphae penetrate into the interior much more quickly than when a longitudinal face of the block is inoculated and with better results. In the latter case more of the exterior becomes overgrown though this is of no special advantage.

In due time, from two months onward in the case of successful cultures, small white hemispherical humps appear here and there on the surfaces of the blocks. The number on different blocks varies from two or three to eight or ten. Their appearance is spread over a considerable period of time, during which some might be produced simultaneously. Some cease growth very shortly after their formation, while others continue for some weeks and then come to a standstill. In these, with cessation of increase in size a thin leathery outer layer is organized. Sectioning reveals the same color zonation of tissues as one sees in that portion of the pileus above the first tube layer in any fruiting body of *F. applanatus*. As a rule one or two humps grow steadily larger at an appreciable rate till they reach their maximum for the growth [illegible] about one inch in diameter in the case of the blocks of the volume used. It was evident that the size depends upon the number of humps in relation to the food supply. In some jars these humps grew superimposed on one another producing quite bizarre shapes. In others the humps appeared more in the nature [illegible] (Fig. 6). In the great majority of [illegible] attained, but in others in the course of some seven to nine [illegible] begin to make their appearance; Fig. 4 shows my first succ[illegible] The deposit of brown spores on the side of the [illegible] shortly after the pored area began to form [illegible] density of the coating spore disc[illegible] the experiment was terminated and the spores examined. They were found to be typical *Fomes applanatus* spores.

In no instance as yet, though by the [illegible] [illegible] were [illegible] in larger chips [illegible]

of *P. applanatus*. The hemispherical form with a small po
appearing in various directions is comparatively common
ch a specimen one may often see another of approximately
e pushing out into a small bracket before developing pore
is a case of more food being within the influence of the lat
flattish cake-like form developed in some cultures is also to be
ure. As well as such occurrences on logs, the writer has co
fruiting body of this shape some eight inches in diameter with
upper surface pored, growing on the ground attached to a sm
urried several inches beneath. Fig. 7 shows one of the most
shape collected from the field.

The experience of all who have cultivated wood-inhabit
throughout their life cycle under artificial conditions has bee
that they find that the fruiting bodies practically never a
normal shape. A few lamellate forms such as *Collybia velutipe*
Costantin et Matruchot), and *Schizophyllum commune* sp
exceptions to this rule, do produce normal sporophores. Th
experience likewise has been that the sporophores of those few sp
have been induced to fruit are not only abnormal in shape but
usually sterile. This has been attributed to various factors
the unnatural conditions of their environment, such as re
supply, light, etc. (Ward, Price, etc.). Probably no general
tion applies, the causes being likely specific for each form. Th
(92) found with certain *Coprini* that sporophore form
inhibited by a damp atmosphere, Bitten found that *Collybia*
develops normally whether aerated or not. *Lentinus lepideus*
in the absence of light (Buller), while
Bitten) and *Stereum hirsutum* (Ward) do equally well in light
There is one important factor, however, that has been overl
experimenters; it has been the practice to use very small
wood in their cultures, and the writer is of the opinion that many
fruit bodies have been due to the fact th
pieces of wood do not afford a sufficient supply of food. Cultu
employed.

V. DECAY.

the agency of fungi hav

as a rule, the gross phenomena alone, or those evident without the aid of the microscope, are sufficiently characteristic to enable the wood pathologist to recognise the causal agent. These phenomena cover a wide range of features. They include, for instance, restrictions as to the species of wood attacked and the selection of sapwood or heartwood, or the absence of such a choice; they include the nature and the extent of the decay within the areas involved—completeness of the destruction varying with different fungi from changes that scarcely affect the commercial use of the wood to complete solution of the wood substance. Then, too, there are changes in color, due to the color of the invading fungus threads, to secretions by them, to secretions by a stimulated host or to chemical changes produced by them; the chemical changes caused by some species result in an extraction of cellulose leaving the wood darker, and in others of lignin, leaving it whiter. The texture of the residual decayed mass, its odour, water content, or mode of fragmentation, are also specific in many cases. Even the method of the dissolution of the cellular elements of the wood, and the formation or otherwise of sheets or strands of mycelium by the fungus in the product of its handiwork are characteristic for most species.

Fomes applanatus conforms to the general rule, and it is of special interest to note in a form that attacks so many different species of host that not only are the phenomena of decay produced by this fungus characteristic but that in the score or more species of host on which observations have been made they are essentially identical in all. It has also been of interest to discover that when *F. applanatus* is acting in living wood it produces one important phenomenon of decay that is not shown when acting in dead wood. Such a difference in behaviour is manifested by several other species, but apparently attention has been rarely called, if at all, to this feature.

The only account of the decay caused by *Fomes applanatus* found in the literature is a brief one by Heald (20) with reference to a disease of the cottonwood ascribed to this fungus. He describes the fungus as attacking certain areas more severely than others, rendering the wood soft and punky in the former and brittle in the latter, and states that chemically the action is one of delignification followed by a partial digestion of the cellulose walls. In describing the rot he says his material showed "the severely infested portions of the wood to be arranged in quite marked horizontal strata. The difference between the two regions (the strata and the sounder intervening wood) is so marked that at the first examination it was thought that the tree was infested with borers, and that they were responsible for this effect". The earlier

characteristic decay produced by the fungus is not mentione
apparently having studied material in an advanced stage of de
indeed, there is a possibility that other fungi were associa
F. applanatus in the stage of decay described by him. He indica
statement that "the naked eye examination of the cut surface a
the presence of characteristic black lines that run in general t
direction . . . The black lines which were mention
prominent feature of the decomposition by the fungus. How
microscopic section as well we believe it in the lumina of the dead
cells." Heald suggests that these deposits represent endeavour
part of the tree to check the advance of the fungus. The writer
assiduous search among hundreds of cases of *F. applanatus* in
field, has been unable to verify Heald's observation on this point
lines are encountered, but cultural or other evidence shows that w
do occur more than one species of fungus is at work. They are p
at the point of contact of two invading fungi in the case of m
of wood-destroying fungi, a phenomenon well known to path ology

Field observations indicate that *Fomes applanatus* usually l
attacks in wounds on a root near the collar or on the trunk at it
that it may with some reason be regarded as the cause of a root
It works inward to the heartwood and thence upward, and a
gresses the decay extends outward involving the lower sapwood
the decay is largely confined to the lowermost few feet of the
may occasionally extend upward some 12 or 15 feet.

The wood attacked very early exhibits a mottled appearan
ciently characteristic to enable the recognition of this fungus lo
fruiting bodies begin to form. The effects produced in heartw
sapwood are the same. This appearance is best described by
tration (Fig. 8). The lighter coloured areas in the mottling, ind
location of the majority of the hyphal threads, though the colou
not to the threads, but to the reduced density of the wood and it
ing consequent on the extraction of lignin. These [illegible]
lacing systems more or less rectangular, with the general di
[illegible]

[illegible]

[illegible]

of decay becomes less and less. The wood substance has been gradually disappearing from these portions leaving localized pockets which may eventually become almost one-quarter of an inch across. Into these spaces, at the same time, the hyphae have been steadily gathering and forming into tough leathery strands which may be picked out in their entirety, leaving channels not unlike larval borings, especially since the original rectilineal directions of the most severely attacked regions have been lost with the progress of the disease (Fig. 9). This feature of the decay agrees with Heald's observation. Since the hyphal core is of the same whitish colour as the surrounding cellulose elements this phase of the work of the fungus is easily overlooked macroscopically. The uniform whitish colour is very late in coming and indicates the final stage of decay. By this time the wood has become very soft and light in weight and rather spongy. No further destruction goes on, the complete disintegration and disappearance of wood substance being always localized.

The mottled type of rot is not restricted to *Fomes applanatus*. Several other fungi produce a mottled rot, but so characteristic in each case as to be distinguishable from one another and from the decay of the form under consideration. Thus, *F. fomentarius* produces a mottled rot but it is a very much finer mottling; with the progress of the disease, however, it early passes into a uniform white rot, which perhaps in most cases could not be identified with certainty at that stage. The mottling caused by *P. squamosus* is very much finer still, and more in the form of white lines, with the general direction tangential, and in dried wood it appears as fine depressed lines; while that of *P.* [illegible] in conifers is also finer, but mostly radially, and since there is complete dissolution locally with no core of fungus threads left, the final result is a sort of pinhole or shot hole effect, as though the wood had been shot through with fine bird shot.

A study of the living wood of trees attacked by *F. applanatus* shows, as I have already indicated, a feature not found in dead wood. I refer to a brownish discoloured zone which marks the extreme limit of advance of the fungus, making the line of demarcation from the sound and yet [illegible] wood very distinct (Figs. 15, 16). In cross section the discoloured region appears as a brown band one-quarter of an inch or more wide, similar in appearance to the band in living wood rotted by *F.* [illegible] though possibly not quite so sharply defined as in the case of the [illegible]. This band is something altogether different from Heald's "black, [illegible] wood" [illegible] is running in a general transverse direction and

which, as has already been pointed out, are commonly encountere
two wood-destroying fungi are at work together.

The dark colour in this band is due to a deposit of so-called
gum", a secretion or a decomposition product of host origin ir
newly attacked by the parasite. A microscopic examinatio
that the "wound gum" is most abundant in the lumina of p
matous cells and in the vessels, though it may be found in an
cellular elements (Fig. 18, Text Fig. 2). It occurs in the form
yellowish brown drops, few or many in a cell, and varying fro
points to masses large enough to occlude the cell cavities. It
absent from the normal uninvaded wood and so it is to be regar
strictly pathological phenomenon. As the anterior margin of t
creeps forward, keeping pace with the advancing hyphae, the p
margin advances with equal rapidity leaving no trace of the disco
in the tissues behind; the "wound gum" is either bleached or ser
part of the food of the fungus; at all events remains of it are not r

by the aid of any of the stains or other
employed in studies of the diseased wo

Tyloses constitute another rem
feature of the brown zone. I have fou
in attacked sapwood and heartwood of
species in which search was made fo
including beech, sugar maple and r
but not in the wood of the apple
crowd the lumina of the vessels, con
filling them as with a continuous grow
the "wound gum" found in the ve
part at least, located in the in-growing
Tyloses do not occur in the sound t
yond the brown band. It is also striki
to a large extent the tyloses are soon de
by the occupying fungus—for a short distance behind the brow
there may be but few traces of them left. A close examina
made to discover whether or not the "wound gum" and ty
might not be formed just before the tissues in question were
by the hyphae [illegible] the evidence obtained negatived an
supposition. The brown band is the first stage in the destru
wood, but more than that, the "wound gum" and tyl
features of importance in interpreting the nature of the fungu
[illegible] point of view will be dealt with in the se
[illegible]

The microscopic features of wood attacked by *F. applanatus* are illustrated in Figs. 10 to 14. The hyphae seem to advance primarily along the medullary rays and vessels, more particularly the former, but all kinds of cells are penetrated. On visualizing the advance of the fungus threads as a whole, one does not perceive any particular evidence of chemotropic attraction exerted on the hyphae. Here and there one meets with appearances in the sections which could be so interpreted, but such are the exception, not the rule. The passage from cell to cell is in no way contingent on connecting pits, for the end of a hypha appears to penetrate the cell wall wherever it may happen to reach it. The hole is small at first, narrower than the normal diameter of the hypha, for the portion of the hypha filling the perforation is more or less reduced. An examination of the tissues taken from the advancing area of decay shows that the cells are perforated with multitudinous holes, the hyphae advancing parallel across the grain in close array. This wholesale perforation is very striking under the microscope and constitutes the first stage in the destruction of the wood. The perforation of the tissue is succeeded by a progressive solution of the cell wall itself. In the neighbourhood of any particular hypha there is a steady reduction of the cell wall so that the originally narrow perforation now becomes a large irregular hole, many times larger in area than at first. With the enlarging of the perforations, contiguous openings frequently merge; a cell wall at this stage presents a very much riddled and corroded appearance. The solution of the cell wall proceeds in a constant manner, but the inner laminae disappear rather more rapidly than the middle lamella. The destruction continues in extreme cases till nothing is left but fragments of the most resistant parts—the angular "gussets" at cell corners and pieces of middle lamellae. This is the stage observed in sections including the local pockets already mentioned.

The first chemical change in the wood during its destruction is a progressive delignification, as shown by the usual chemical tests for lignin and cellulose. Sections treated with phloroglucin and hydrochloric acid show a very faint red colour in the primary areas of attack; the colour increases in intensity in the tissue farther and farther away from these areas. On the application of chlor-zinc-iodide solution the wood takes on a bluish colour which is deepest in the primary areas of decay. But the delignification is never wholly complete, for in the most thoroughly rotted wood, in the centre of large strands of hyphae there are always some fragments which still give the reaction for lignin. The cellulose resulting from delignification is in turn finally dissolved, but only usually completely so.

In working out the diagnostic marks of the decay caused *applanatus* certain pitfalls have been discovered when checki results over by culture tests—pitfalls that are doubtless to be encou in the study of all similar fungi, and which must be carefully av descriptions of decay are to be of value. The most important o has to do with the recognition of the action of secondary agencies mere finding of a fruiting body on a diseased area is by no means ev that all of the effect apparent is due to this one fungus, nor, ev such a conclusion be extended to most cases in which the effe uniform accompaniment of a certain species of fruiting body. Of where the rot is of a very distinctive type such an association accepted as fairly adequate evidence, though even in such cases is necessary. Most of the wood-destroying fungi act rather many years often elapsing before the sporophores appear, and duri time secondary purely saprophytic bacteria and fungi have ample tunity to make their entrance. Cultures made from most woo advanced stage of decay almost invariably reveal the presence secondary agencies, thus raising a question as to the value of descriptions of decay which so commonly are based on late stag leading to the conclusion that some of the culminating features are often to be attributed to other organisms than the primar In such cases, doubtless the earlier marks are much more distinct of greater value in a diagnosis of the disease than the later. Th tainly applies to *F. applanatus*.

In correlating decay and causal agent in the case of *F. app* the most extensive tests were made on Lombardy poplar—a freshly tree that had borne fruiting bodies of *F. applanatus* for years an of no other species of fungus. Pieces taken from the interior of selected from the upper limits to which the disease had progresse which showed the characteristic mottling, were cultured on potat and on sterile pieces of wood through to fruit and spore product that no question remained as to the identity of the causal age cultures made from such a source contamination by bacteria o forms rarely appears. Cultures made from mottled areas in man woods likewise always showed an almost constant freedom fron fungi and bacteria. On the other hand in cultures made from woo uniform white stage of decay bacteria and other forms practically appear. It is reasonably certain that we may conclude that co destruction in the case of *F. applanatus* after the uniform whit reached may in part be the work of combined agencies.

VI. PARASITISM

The distinction between parasitic and saprophytic fungi is based on the nature of their nutrition. But between strict parasites, which are completely dependent on living hosts, some of them such as the Uredineae not even cultivable on dead substrata, and strict saprophytes, which undergo none of their development in vital connection with a living host, there is a vast assemblage of forms that exhibit the possibilities of either a parasitic or a saprophytic mode of existence. Further, these forms, in their greater tendency or preference towards the one or the other relation, present such a variation that the extremes of strict parasitism and strict saprophytism are bridged by a closely intergraded series. These intermediate forms have been provisionally classified as hemisaprophytes or facultative parasites, that is, those normally saprophytic but which may live at least partially as parasites, and hemiparasites or facultative saprophytes, that is those normally parasitic but which can live for a time as saprophytes. As an example of the first class might be mentioned *Polystictus versicolor*, one of our most widely distributed species and most cosmopolitan in respect to its choice of hosts; it is classed as one of our commonest saprophytes, but occasionally exhibits parasitism (described by von Schrenk (40) as a wound parasite causing a heart rot of *Catalpa speciosa* and lilac). On the other hand we have forms such as *Fomes annosus* (*T. radiciperda*) which, while an undoubted parasite of conifers, occurs also as a typical saprophyte on converted timber. But this classification into hemi-forms is at best an approximation and is valueless in the case of many forms because of our uncertainty with regard to their exact nutritive relation, or because the two potentialities are so evenly balanced in their constitution. Such an even balance is to be found in forms like *Fomes igniarius* or *Polyporus ulmarius* which continue growth and produce fruiting bodies long after the death of the living hosts.

But in practice any imperfection in the classification of this intermediate series is of little importance in comparison with the ability to distinguish the facultative parasite from the strict saprophyte, for the one wrongly classified and so removed from critical surveillance is likely in consequence to be allowed to continue its destructive work unchecked, and conceivably might even be unsuspectingly brought into new conditions under which it would prove to be a troublesome pathological problem. This applies with especial force to the fungi that occur on trees. On such large plants considerable amounts of dead tissue may be tolerated by them without seriously impairing their health, and these dead

areas may, and often do, serve as the pabulum for many kinds
Obviously it is a matter of considerable consequence to distingui
these fungi these that are strictly saprophytic and unable to pas
the dead areas from those that are capable of encroaching
tissues and of insidiously though more or less certainly encro
the life of their host. Unfortunately in a very large number
there are no known marks whereby the potentially parasitic form
recognized with certainty. This difficulty has been encountere
students of tree diseases, but no very satisfactory applicable sol
been proposed. Distinguishing data have been proposed
investigators in the field but they fall short when an attempt
to apply them. This is aptly illustrated in a review of dis
deciduous trees by von Schrenk and Spaulding (41). These
make two groups of wood-destroying fungi, viz., wound pa
those fungi gaining entrance through wounds or branch stubs
centre of a tree and decaying a heart rot which extends outwards t
the sapwood and eventually kills the tree" . . . . and
phytes—"which grow on dead wood, including both wood
from the living tree, and in some cases dead heartwood or
actually exposed to the air but still forming a part of th
tree". The classification here is satisfactory, but an att
recognize the parasite from the directions given for its re
leads to much uncertainty. No better illustration of this could
than that of *F. applanatus*.

Among the terms attacking trees there has been no great
tainty and difference of opinion with regard to its ability to
parasite than in the case of *Fomes applanatus*. Thus, Spaul
says "*Fomes applanatus* attacks dead wood in living trees,
when the trunk has been injured, causing large wounds w
favorable to its entrance. It is not, however, a true heart-rottin
as its attacks are made on dead sapwood rather than dead hea
Weir (50) after mentioning its occurrence on dead conifers, sa
occasionally taken from dead parts of living trees". Hedge
writes "*Fomes applanatus* has rarely been found fruiting on liv
a statement borne out by the author's experience. Th
to verify the view of von Schrenk and Spaulding that this fun
not cause a disease in the trees that the rots produced by *F. igni*
F. fraxinophilus are diseases. It attacks readily both sap an
entering the sapwood of dead exposed tops or as dead areas at th
trees." But two years later he (21) says "after making furthe
observing the effect of this fungus upon living trees, the writer h

to the conclusion that very frequently it attacks both the sap and heart of many living trees. (No statement is given of the grounds on which this conclusion is based.) It is able to enter such trees only through wounds. In the majority of instances, however, the fungus acts only as a saprophyte". Heald considers it a facultative parasite, stating "it would seem probable that the fungus is not able to attack young healthy trees (of cottonwood), but that it can become parasitic on older trees in which the vitality has been considerably lowered, or that have reached the maximum of their development". Von Schrenk and Spaulding dissent from this view—"In many recent descriptions of diseases of forest trees reference is made to fungi which in the opinion of the writers must be considered strictly saprophytic forms which occur only on dead wood. A striking instance of this is *Fomes applanatus*. This fungus is frequently found on living trees, but a careful examination always shows it to be growing on wood which is actually dead, and generally on the outer sapwood. So far as the writers have been able to observe *F. applanatus* does not cause what may be called a disease of living [illegible] The same is true of many other fungi. The writers believe, [illegible] that most of these forms, if not all, will not grow on a tree until it has already been so weakened by other factors that to all intents and purposes it is dying or dead, with the possible exception of cases where the fungi grow on dead patches of wood caused by some injury, as in the case of trees injured by fire". Neuman (33), after speaking of finding the fungus growing out of wounds in the trunks of living oaks and cottonwood, states "A young apple tree had been looking sickly for the past two or three years, but I found no external fungus growths upon it until a pileus of *Fomes applanatus* appeared on the trunk. The heartwood of the tree was badly decayed . . . . and the fruiting body was attached to the living bark as though it was a parasite".

In attempting to solve the problem as to whether or not *F. applanatus* may act as a parasite I have followed three lines of inquiry: first, evidence of apparent parasitism as judged from the mode of its occurrence and the fate of its hosts (the only kind of evidence alluded to in the literature reviewed above); second, a direct investigation of the invaded tissues of the living host to determine whether or not it could be established with certainty that these tissues were living, and if so, whether or not their subsequent fate was contingent on the action of the occupying fungus; third, the results of inoculating healthy trees with the mycelium [illegible] of the fungus.

Living trees of nearly all the common broad-leaved species have been [illegible] bearing sporophores and in some localities the percentage [illegible]

[illegible]

That this struggle between host and parasite may sometimes persist over a long period of years is certain, and the termination of the struggle is very largely determined by the resisting powers of the host. Apparently, in some cases, the host seems able to hold the parasite in check almost indefinitely, counterbalancing by the season's growth what it loses by the extending inroads of the fungus.

The most practicable control measures in the case of park, street, and fruit trees would seem to be the building up of the vigour of infected [illegible] the prevention of the spreading of the disease to new hosts by [illegible] the formation of fruiting bodies. Surgery has been largely employed with such trees, but to be successful must be absolutely [illegible]

VII. SUMMARY

1. *Fomes applanatus*, a perennial polypore of wide distribution and of common occurrence in North America and in Europe is responsible for the decay of very large quantities of wood annually. It attacks practically all deciduous species and several coniferous species, both dead wood and living trees. This fungus, heretofore commonly regarded as a pure saprophyte, has now for the first time been comprehensively studied; the investigations recorded in this paper have followed along three main lines of inquiry: (1) a study of the morphology and the ecology of *F. applanatus* and of the action on its host; (2) a determination of its etiological relationships by culture methods, and a testing of the applicability of such methods to a study of the timber destroying fungi; (3) an investigation of the possibility of finding criteria by which we may distinguish parasitic action on wood from saprophytic.

2. *Fomes applanatus* produces basidiospores only; conidia are not produced by the mycelium, nor, as is commonly affirmed, on the upper surface of the sporophore. The basidiospores are not of the ordinary type; each consists of a yellow, papillate, thick-walled chlamydospore within a thin hyaline wall. The so-called "truncate" base is in reality the apical end of the spore.

3. Spore discharge is enormous and continues for by far the longest period recorded for fungi. It is continuous day and night for about six months, visible from vigorous fruiting bodies as spore clouds. Discharge is not affected by variations in light, humidity of the air, or temperature within very wide limits; frost causes an instant cessation and thereafter there is no further spore fall until a new set of pores is organized.

The spores were not found to retain their viability for more t
6½ months. They germinate in water and various other media wi
48 hours after sowing, but the percentage of viable spores is very
and their behaviour with respect to germination is erratic.

3. No difficulty was experienced in culturing *F. applanatus* on
ficial media or on wood.

Three parallel series of cultures on wood were carried throug
-porulation with mycelium obtained from (*a*) spores, (*b*) pieces of sp
phore, (*c*) pieces of diseased wood.

4. Wood rotted by *F. applanatus* exhibits a mottled appear
sufficiently characteristic to permit of its recognition when comp
with other rot.

In the case of living wood the area of attack is delimited by a
dark band.

Histologically, the decay is characterized by a perforation and
ion of the elements culminating in disappearance of the tissu
localized pockets into which the mycelium gathers forming strands

Chemically, the change is one of delignification followed by a
gressive solution of the resultant cellulose wall except for a few res
tracted.

In the later uniform white stage of decay, the threads of *F. applan*
were always found to be accompanied by other destructive age
bacteria or fungi.

5. The particular type of decay in timber due to *Fomes appl*
has now been linked with its causal agent by actual culture.

6. *Fomes applanatus* has been proved to be a wound par
southern Ontario at least is one of the commonest and most destru
of this type. The proof rests on three grounds: (*a*) the convention
applied to other such fungi—the mycelium works upward most
by the way of the heartwood causing a characteristic decay and
into the sapwood, eventually reaching the cambium, and is appa
the cause of the death of the tissues traversed by it; (*b*) a broad
band is present in the wood of living trees along the advance line
invading mycelium of this fungus. Within this band there is a c
production of brown wound gum and an excessive multiplicat
tyloses. This band steadily moves forward with the advancing h
the tyloses and wound gum being destroyed by the mycelium al
posterior margin as rapidly as they are formed along its anterio
The tyloses (and possibly the wound gum also) certify to the livi
of the invaded tissues; their production can be ascribed only
influence of the fungus, and the mycelium [illegible] and the

demonstrates directly its ability to act as a parasite; (*c*) inoculations with the sterilized mycelium of *F. applanatus* into living trees resulted in an extensive browning of the inoculated wood with a multiplication of tyloses such far in excess of similar phenomena due to traumatic complication.

7. The occurrence of wound gum and the multiplication of tyloses in wood marking the advance of a wood-destroying fungus in a living tree would appear to furnish an unerring criterion for the recognition of the fungus as a parasite.

The investigation was carried out in the Botanical Laboratories, University of Toronto, under the direction of Professor J. H. Faull, and to him the writer is indebted for constant encouragement and advice.

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EXPLANATION OF PLATES

Fig. 1. Illustrating great variation in width of sterile band in *Fomes applanatus;* × 2/3.

Fig. 2. *Tilia americana*, 14 days after inoculation with agar bearing mycelium; × 7/8.

Fig. 3. The same test with *Tsuga canadensis*, thus illustrating relative immunity of coniferes; × 7/8.

Fig. 4. *F. applanatus* cultured from spore to spore under artificial conditions throughout (7 months). The spore deposit is to be seen on the glass and on the cotton batting. Jar not opened between inoculation and sporulation; × 7/9.

Fig. 5. Enlargement of pored surface of the preceding; × 5.

Fig. 6. Showing sterile "humps" usually obtained in cultures; × 4/5.

Fig. 7. A freak form assumed by *F. applanatus* in nature; × 1/4.

Fig. 8. Lombardy poplar attacked by *F. applanatus*, in an early stage.

Fig. 9. A very advanced stage of the decay, in beech; × 1.

Fig. 10. Cross section of beech wood showing first stages of decay; elements perforated and reduction of wall thickness just beginning; × 212.

Fig. 11. An advanced stage of the same; elements gone locally except for more resistant portions; × 212.

Fig. 12. Longitudinal section corresponding to Fig. 10, and showing extensive perforation; × 212.

Fig. 13. Longitudinal section of advanced stage of decay; perforations have merged and walls very much reduced in thickness, with some entirely gone; × 212.

Fig. 14. Composite drawing to illustrate successive steps in decay.

Fig. 15. Radial view of block from living hard maple attacked by *F. applanatus;* dark band marks advance line of fungus working outwards from the heartwood; × 1½.

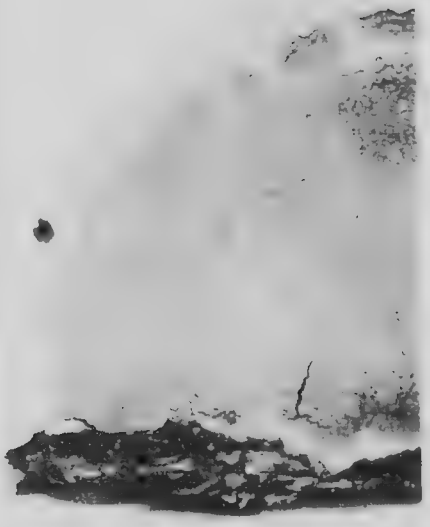
Fig. 16. Same feature in red oak.

Fig. 17. Piece from trunk of sound young hard maple tree 12 months after inoculation with *F. applanatus;* the discoloured volume has been attacked; note that the wood laid down after the experiment was begun resisted attack; × 1.

Fig. 18. Radial view in region of dark band shown in Fig. 15; on the right tissue vigorously attacked, and on the left sound tissue showing tyloses and wound gum; × 212.

Fig. 19. Cross section of a sugar maple trunk showing affected areas some distance above and below the point. [illegible]

Figs. 20 and 21. Illustrating the results of inoculation on young hard maple trees. Fig. 20 shows the *n.a.*, *n.a.m.* discoloration obtained by inoculation among all the controls in all the test trees. [illegible]



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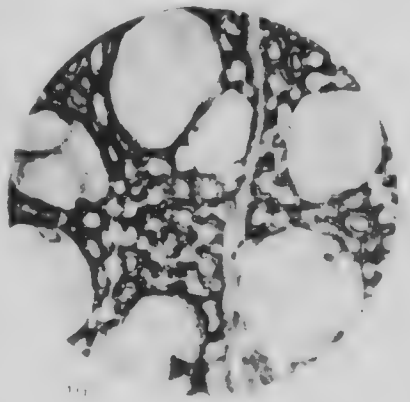

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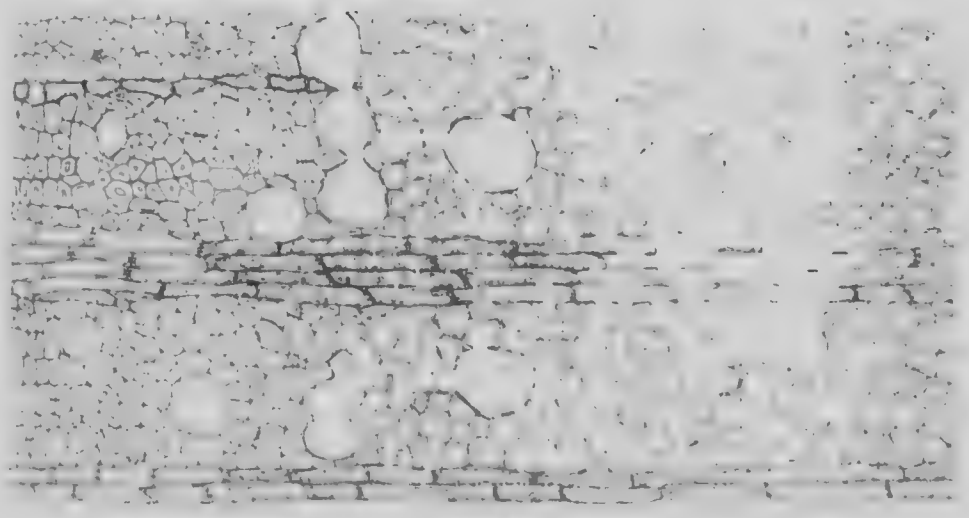

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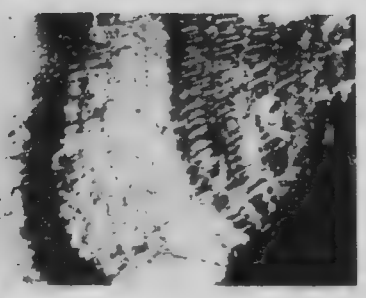

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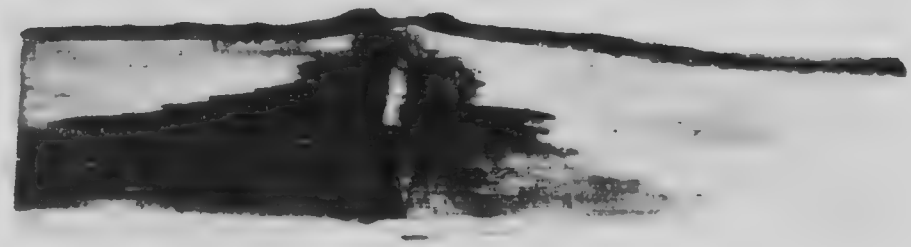

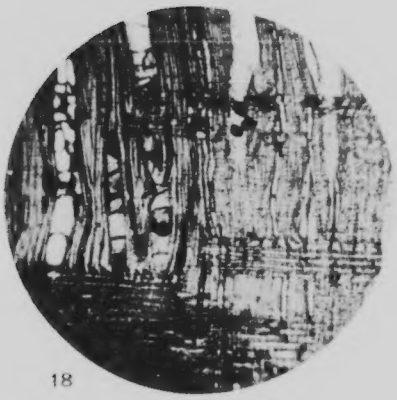

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